Feeding of mature cod (*Gadus morhua* L.) at the spawning grounds in Lofoten

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Abstract

Numerous studies state that cod (*Gadus morhua* L.) do not feed during the spawning period. However, this more or less established fact has rarely been investigated in the field. In this study content of stomachs from Northeast Arctic cod (NEAC) and Norwegian coastal cod (NCC) sampled from the spawning ground in Lofoten over a 10-year period (1996–2006) were examined. The occurrence of food in stomachs of spawning cod, stomach fullness, diet composition, as well as variation in these variables between NEAC and NCC, year and sex were analyzed and compared. The analysis shows that cod do feed, even when they are in a spawning state. NCC had lower proportion of empty stomachs and the stomachs were fuller than those from NEAC. Females had lower proportion of empty stomachs than males and their stomachs were in general fuller than those of the males. Herring (*Clupea harengus* L.) dominated in the cod diet. However, cod consumption of herring on the spawning grounds seems to be a minor source of mortality on herring. Even though spawning cod do feed, the proportion of empty stomachs was higher and stomach fullness was lower, compared to stomachs taken from NEAC in the Barents Sea.

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Introduction

In some early studies of otolith structure and life-history characteristics, Rollefsen (1933, 1934, 1935) points out a direct connection between the appearance of a particular zone in the otoliths and spawning of cod based on the "fundamental change occurring with the ripening of the gonads, the spawning, the fast during spawning, the spawning migration and the stay in a new habitat" (cited from Rollefsen, 1933). Since then, several authors have referred to these findings and it has more or less been established as a fact that cod do not feed in the spawning period (i.e. Bergstad et al., 1987; Jobling, 1994; Kjesbu et al., 1998). However, to our knowledge, neither Rollefsen (1933) nor any later studies have actually conducted detailed analysis of the stomachs from cod at the spawning ground. The combination of lack of empirical support, knowledge about traditional fishing techniques with baited hooks in the spawning area and personal field observations of stomach content of spawning cod, inspired us to take a closer look at this "common truth".

The cod along the Norwegian coast and in the Barents Sea are divided into two types, the Northeast Arctic cod (NEAC) and the Norwegian coastal cod (NCC, Berg and Albert, 2003). NEAC is the major cod type in the Northeast Atlantic and mature individuals conduct long migrations from the cold feeding grounds in the northern and eastern parts of the Barents Sea to the warmer spawning areas along the coast of Norway (see Ottersen et al. 1998 for references). In contrast, NCC do not undertake large-scale seasonal migrations (Jakobsen, 1987), and may experience an opposite cycle in temperature as compared to NEAC (Godø and Michalsen, 2000). Like most spring spawners, both NEAC and NCC build up energy reserves during summer and fall, which are later used for maturation, migration and spawning (Jobling, 1982; Lambert and Dutil, 2000). Differences in consumption rates and stomach content between females and males have been reported (Fordham and Trippel, 1999).

Spawning of NEAC and NCC takes place at several locations along the coast of northern Norway, but the most important spawning area is off the coast of the Lofoten peninsula (Sundby and Bratland, 1987, Figure 1). Here the spawning areas of the two cod types overlap (Jakobsen 1987; Berg and Albert, 2003). The majority of all cod eggs are spawned during March and April, with a peak around the first days of April (Ellertsen et al., 1981). It has been reported that cod spawn in the thermocline between 4 and 6 ^{o}C, but long-term hydrographic conditions together with short-term atmospheric forcing, influence the depth of the thermocline layer and hence also the depth where the spawning occurs (Ellertsen et al., 1989).

The objective of the present study is to determine whether cod feed in the spawning period and, if so, which prey species they feed on. We test for differences in feeding between spawning NCC and NEAC, and between males and females. This is primarily accomplished by analysing stomach data from 10 years of field observations in the main spawning area for Northeast Arctic cod. We furthermore try to quantify the consumption in the main spawning period, and investigate how important this consumption is as a source of mortality for herring. We also compare feeding of NEAC in the spawning period with feeding in the summer and winter in the Barents Sea.

Material and methods

Annual abundance surveys on Northeast Arctic cod have been conducted at the main spawning ground in Lofoten in the period March-April (see Korsbrekke, 1997). These annual cruises have covered the same geographical area, each year from 1982 to present time (Figure 1). Even though they primarily are acoustic surveys, bottom- and pelagic trawl hauls have been carried out for species and size verification and biological sampling for population dynamic studies.

Stomachs of cod have been collected at trawl stations on a regular basis on these cruises since 1985. In the present study only field observations from 1996-1999 and 2001-2006 had adequate number of stations (> 10) and stomach samples to be included in our analysis. Also, only mature cod are included in the analysis (data from maturity stages 2, defined as large gonads, visible eggs and male gonad products and maturity stage 3, representing running gonads, see Kjesbu, 1990 for details). Most of the stomach data were from bottom trawl hauls, but some were from pelagic trawl hauls (Table 1). Stomachs of fish that had regurgitated were not included. Each stomach was frozen separately and data on length, age, weight, sex, otolith type (see below), and maturity stage of each individual predator was recorded. Fish prey was identified to species when possible, and the total length was measured, rounded downwards to the nearest cm. The methods used for stomach sampling, analysis and data recording are described more fully in Mehl (1989) and Mehl and Yaragina (1992). The mature fish made up 85% of the total number of fish from which stomach samples were taken. In addition a distinction between Northeast Arctic cod (NEAC) and Norwegian Coastal Cod (NCC) was conducted based on the structure of the otoliths (Mjanger et al., 2005).

Data analysis

We used the proportion of empty stomachs, total fullness index (TFI) and partial fullness index (PFI) to quantify cod feeding in the Lofoten area. The Partial Fullness Index (Lilly and Fleming, 1981) corrected for differences in stomach content related to fish size and is defined by:

$$PFI = 10^4 * W_s/L^3$$

where W_s is the wet weight (g) of prey species *s* in the cod stomach and L is the length (cm) of the cod. Similarly,

$$TFI = 10^4 * W_t/L^3$$

is the Total Fullness Index, where W_t is the total wet weight (g) of prey in the cod stomach.

The centers of mass of herring occurring in stomachs of cod were calculated by year, based on the value of PFI of herring per station. The longitudinal and latitudinal coordinates of the centers of mass of distribution are averages of the coordinates of each trawl station weighted by the value of PFI of herring. We tested for differences between NEAC and NCC, year and sex on cod feeding in Lofoten using three way mixed effects ANOVA (Proc Mixed and the glimmix macro, SAS version 9.1, www.sas.com). Cod length was entered as a covariate. Station was entered as a random variable in the statistical model, to account for statistical dependencies between cod stomach samples taken from the same station (see Bogstad et al. 1995). When analysing the proportion of empty stomachs we used a logistic link function and binomial error.

Sample sizes by year, sex and cod type are given in Table 1. Males constituted 65% of the cod sampled at the Lofoten cruise. The proportion of males in the bottom trawl was 0.67 (95% confidence interval: 0.65-0.68), whereas it was 0.54 (95% confidence interval: 0.50-0.59) for the pelagic trawl. Because of small sample sizes of pelagic hauls, data from both trawl types were pooled in the analysis.

We tested for seasonal variation in feeding of NEAC by performing a two way mixed effects ANOVA using season and year as fixed factors, and station as a random variable. Feeding of cod was quantified using TFI and proportion empty stomachs. When analysing the proportion of empty stomachs we used a logistic link function and binomial error.

In addition to the data from the spawning season (Table 1), we included data from two surveys run in the Barents Sea: the combined acoustic and bottom trawl survey for demersal fish in the Barents Sea in winter (Jakobsen et al., 1997), now run jointly with PINRO in February, and data from the demersal fish survey in the Barents Sea and Svalbard area in summer, now run as the joint IMR-PINRO ecosystem survey in August/September. We included only cod larger than 50 cm in this analysis. We included the years 1996, 1999, 2003-2005 because these years had good coverage in both summer and winter. The cod stomach samples were taken from cod sampled from demersal trawls. On these surveys, a maximum of five stomachs per five cm length group of cod is sampled per station. The number of stomachs samples by year, sex and season in the summer and winter survey is presented in Table 2.

We also calculated the consumption by cod during the spawning migration based on the stomach samples and a model for gastric evacuation rate. We used an approach similar to Bogstad and Mehl (1997), who calculated the consumption by cod in the Barents Sea. The method is described in Appendix 1.

Results

The size distribution of spawning females and males differed, with males being smaller than females and NCC being smaller in length than the NEAC (Figure 2).

NCC had lower proportion of empty stomachs than NEAC (0.64 vs. 0.68). Females had lower proportion of empty stomachs than males, but there was a significant interaction between sex and year; the sex difference was pronounced in 1996 and 2001, but not the other years (Table 3, Figure 3). The data do not allow us to investigate possible reasons for this difference, like for example difference in geographic distribution of cod sex and herring. No other interaction terms were significant.

The results for TFI were consistent with the pattern for the proportion of empty stomachs (Table 3, Figure 4). Stomachs of NCC were fuller than stomachs of NEA (0.44 vs. 0.39, Figure 4). There was no effect of cod length on TFI and no interaction terms were significant (Table 3).

Herring (*Clupea harengus*) was the most important prey species, followed by Norway pout (*Trisopterus esmarkii*) for both NEAC and NCC (Figure 5). PFI of herring did vary significantly by year (Table 3). No interactions were significant (Table 3). The yearly variation in PFI of herring could partly be due to variable degree of digestion, leading to variable level of species identification (Figure 6). However, when pooling data on herring and un-classified fish, assuming that most of this is herring, year was still significant (p<0.0001). There has been a change in the spatial distribution of herring in cod stomachs over the years (Figure 1) that might be due to changes in the geographical distribution of herring, but we do not have data to investigate this relationship. The length distribution of herring in cod stomachs (Figure 7) shows a significant correlation between cod size and herring size (r=-0.27, p=0.02, n=77).

There was no sex difference in TFI and the proportion of empty stomachs in winter or summer (one-way mixed model ANOVA sex effect, TFI winter: p=0.63, summer: p=0.34, proportion empty stomachs winter: p=0.11, summer: p=0.09). TFI values and proportion of empty stomachs were compared between spawning NEA cod at the spawning ground in Lofoten in April, cod >50 cm in Barents Sea in February, and cod >50 cm in Svalbard and Barents Sea area in August-September 1996, 1999, 2003-2005. There was a significant effect of season (winter, spawning season in spring and summer) and year and a significant interaction between season and year on the proportion of empty stomachs (Table 4). There was also a significant effect of season and a significant interaction between season and year on TFI (Table 4). TFI was lower and proportion of empty stomachs was higher at the spawning ground in all years. Generally, TFI was higher and the proportion of empty stomachs was lower in summer compared to winter (Figure 8 and Figure 9). However, in 1999 and 2003 the difference between summer and winter was negligible.

The consumption of the various prey items by year is given in Table 5 (NEAC) and Table 6 (NCC). The biomass output through natural mortality (MOB) for herring is given in Table 7, together with the calculated consumption of herring. Also the proportion of the MOB corresponding to the calculated consumption of herring by cod is shown. The consumption of herring by cod during the spawning period of cod is <100 thousand tonnes in all years. This is small compared to the MOB of herring (between 1 and 7% of the MOB).

Discussion

In Canadian waters, cod generally move from offshore wintering areas, with a near absence of food intake to inshore spawning areas where prey is abundant (Comeau et al., 2002). Such variability in seasonal feeding indicates that stock-specific empirical data are needed to reliably assess seasonal growth patterns in cod. In this study we did not consider the effects of the development of gonads, migration or the environmental changes on the otoliths, but simply investigated whether cod in a spawning state do feed, how much and on which species. After analysing 5258 stomachs of spawning cod, collected over a period of 10 years at the spawning grounds in Lofoten, it is clear that cod do fed, even when they are in a spawning state, but that NEAC feed less actively during spawning compared to other times of the year.

Differences between NEAC and NCC

Even though they were caught in the same area, our study has showed that NCC had lower proportion of empty stomachs and also fuller stomachs than NEAC. The diet was also slightly more diverse than for NEAC, where close to 50 % of the stomach content consisted of herring. To understand why there is such a difference in feeding between the two cod types, more detailed studies on the distribution, life history traits, and feeding ecology of the two cod types are needed. However, the larger proportion of invertebrates in the more stationary NCC diet could be a reflection of its smaller size (e.g. Link and Garrison 2002) or difference in habitat use, compared to NEAC.

Fish of the two cod types are distinguished through otolith morphology and the cod type separation criteria developed by Rollefsen (1933 and 1934) are still used (Mjanger et al., 2005). This is based on differences in shape between the two innermost translucent zones. Also spawning zones in the otoliths are used to determine the age at sexual maturity based on

identification of narrower opaque zones with conspicuous clear translucent band. Rollefsen (1933) suggests that these zones are result of physiological changes in the fish during maturation and both NEAC and NCC deposit these zones. However, identification of otolith spawning zones is, up to current time, only done by Norwegian and Russian age readers. Thus, it is clear that the physiological basis for spawning zone formation is poorly understood and that this assumption should be attempted validated or critically tested. Such a validation will also be of great value to study the process of skipped spawning in fish populations (Rideout et al., 2000; Jørgensen and Fiksen, 2006) and should include analyses to check for possible sex differences, as timing of spawning migrations.

Sex differences in feeding and spawning

We found that males were smaller than females, which is consistent with existing knowledge on sexual differences in growth and maturation (Ajiad et al., 1999). Further, females feed more on the spawning ground than males, but no sex difference in winter or summer feeding was found. The process of egg batch production in cod is a strenuous process, where after the release of a batch there occurs mobilization of protein and fat from the muscle and liver to the ovary (Kjesbu et al., 1998). In a study on non-migrating NCC, (Eliassen and Vahl 1982a; b), the effect of gonad production was investigated. They estimated that gonad growth could account for only 10% of the energy lost from cod carcass and liver between January and April. They did discover a sex difference in liver weight, with the occurrence of smaller livers in male than female cod. This was assumed to be a consequence of the observed earlier start of gonad growth in males than in females. However, the conclusion was made under the assumption of cessation of feeding in this prespawning period.

Another aspect of gonad growth and feeding was studied by Hroar et al. (1983). They suggest that the feeding activity could be affected due to less space available in the body

cavity for food, or possibly associated with a change in hormone levels during spawning, which might reduce an individual's appetite. Since feeding habits of males in our study were suppressed during spawning to an even greater degree than observed in females, the theory of lack of space does not seem convincing. Also Fordham and Trippel (1999) found that females consumed greater quantities of food than males during both winter and post spawning periods. This is supported by the fact that in a large number of fishes, the females grow not only larger but also faster than the males (Ajiad et al., 1999) despite their production of large amount of gonad material (Lambert and Dutil, 2000). Clearly, female growth does not suffer from reproductive drain, space in the body cavity or lack of appetite.

We noticed that a higher proportion of males are caught by the bottom trawl than by the pelagic trawl. Also Rollefsen (1954), working off the coast of the Lofoten islands, found that the sex ratio varied, depending on the sampling gear used. Morgan and Trippel (1996) and Morgan et al. (1997) suggest that the skewed sex ratio is at least in part determined by a sex dependent vertical distribution, which will turn out as sex selective gears. Vertical separation of sexes can probably be explained by the mating system (Nordeide and Folstad, 2000), where mature males have been reported to aggregate at the spawning ground whereas females seem to be distributed peripherally or above to the male aggregations (Morgan and Trippel, 1996; Nordeide, 1998). When ready to spawn, females enter male aggregations and return after spawning (Brawn, 1961; Hutchings et al., 1999). Laboratory studies have shown that during the reproductive period, there is aggression between males defending "territories" (Brawn, 1961; Hutchings et al., 1999). This sexual difference in spawning behaviour might also explain the difference in stomach content, where females will be less aggressive and have more time available to encounter available food.

NEAC feeding, in time and space

The overall proportion of empty stomachs was higher (71%) and the average TFI value was lower (0.34) at the spawning grounds, compared to stomachs sampled from NEAC in the Barents Sea in the same years (25% and 1.43 respectively). Seasonal variation in cod metabolism with highest metabolic rates during spring, due to migration, spawning and higher temperatures in the spawning area than in the feeding area (Pedersen and Jobling, 1989), could lead to faster digestion and a higher proportion of empty stomachs. However, this complex process has been poorly studied, and it is therefore difficult to evaluate the potential importance metabolism on the proportion of empty stomachs.

Geographical and temporal variation in prey availability, with less food available in the spawning areas at the time of spawning compared to the Barents Sea in summer and winter, or higher density of cod aggregating at the spawning areas, could both cause food competition and less feeding at the spawning ground. The coastal areas are assumed to be less productive than the Barents Sea (Sakshaug et al., 1994). However, in some of the fjords along the coast, large schools of adult herring aggregate during winter, while they migrate out in the open sea during spring, about the same time as the spawning of cod. The Norwegian Spring Spawning Herring (NSSH) is a large oceanic stock with spawning area, located along the Norwegian coast (Misund et al., 1998). Since 1987, a fjord system close to the main spawning areas of cod, has been the over wintering ground for herring (Toresen and Østvedt, 2000). The herring enters the area in the beginning of October and start the migration out of the fjord system and to the more southern spawning grounds in January (Røttingen, 1992). The occurrence of overwintering of herring in this area may have had an influence on cod, not only as an increase in food availability but also in timing and area chosen for spawning.

The predominant fish species in the ecosystem of the Barents Sea are cod, capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*).

Cod is believed to be the main fish predator on capelin and young herring (Bogstad and Mehl, 1997; Bogstad et al., 2000). The geographical distribution of capelin during its spawning migration does only occasionally extend as far southwest as the Lofoten area (Ozhigin and Luka, 1985). The highest food ratios for cod in the Barents Sea are found in the area close to the polar front during summer and close to the coast of northern Norway and Russia in the first part of the year when the capelin migrate to the coastal areas to spawn (Orlova et al., 1995).

NCC has been found to feed actively during winter (Hop *et al.*, 1992; 1993). In Balsfjorden, northern Norway, the food intake (indicated by stomach fullness) did not appear to decline during winter (Klemetsen, 1982), nevertheless the liver weight declined between January and March (Eliassen and Vahl, 1982a). On the other hand, studies from the North Sea has shown that stomach fullness is lowest during January to March (Daan, 1973; Hislop, 1997), which is more in accordance to our results on seasonal variability in stomach content of NEAC. Such variability in food intake indicates that stock specific data are essential to understand the seasonal growth pattern seen in the otolith structure.

Concluding remarks

Feeding habits of cod during spawning could have implications for abundance surveys, aquaculture, bioenergetic models, multispecies approaches, considerations about gear efficiency and could improve the scientific basis for management of the complex mixed fishery of Atlantic cod in the Lofoten area. Progress in understanding the causes of growth variability in cod has been hampered by incomplete knowledge about the growth implications of seasonal life-history events like spawning and reproduction (Schwalme and Chouinard, 1999). By further assessing the foraging habits during spawning we might be able to more

fully understand the feeding habits of cod and how these change under various conditions or states.

In defence of Rollefsen's (1933) work it should be noted that the spawning stock biomass was estimated to be more than twice as big in the early 1930s as in the late 1990s, namely 1.2 million tonnes compared to around 0.5 million tonnes (ICES, 2006a; Hylen, 2002). With higher density at the spawning ground the probability for finding food would therefore be lower and it may have looked like the cod voluntarily entered a period with no feeding. Based on the results from our study, it is quite clear that cod do feed, even when they are in a spawning state, if there is food available.

Acknowledgements

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Appendix 1. Method for calculating the consumption by cod.

The annual prey consumption by NEAC in the Barents Sea for the period 1984-2005 is calculated by ICES (2006a), using the method described by Bogstad and Mehl (1997). In those calculations, the mature NEAC are assumed to be outside the Barents Sea during the spawning period (i.e. three months during the first half of the year), and the prey consumption by NEAC during that period is not included in the consumption estimates. Using the stomach content data from the Lofoten survey described above, we calculate the annual prey consumption by cod during the spawning period by assuming that the stomach data from the Lofoten survey are representative for the diet of mature NEAC and NCC during a 3-month period. We used the abundance of mature NEAC and NCC from the 2006 stock assessments made by ICES (ICES, 2006a) and estimated the consumption by cod using the methods described in Bogstad and Mehl (1997). The annual consumption of prey group p by mature cod of type s (NEAC or NCC) and age a during the spawning period in year y is then given by:

$$C_{y,s,a,p} = N_{y,s,a} O_{y,s,a} R_{y,s,a,p} \text{ x 24 x 91.25} \qquad (1)$$

where

$N_{y,s,a}$: Number of cod of type s and age a at 1 April in year y. This is found by assuming a constant total mortality during the year and reducing the number of cod at the beginning of the year by one-fourth of the yearly natural and fishing mortality.

$O_{y,s,a}$: Maturity ogive for cod from type s of age a in year y

$R_{y,s,a,p}$: Consumption (g/hour) of prey p by each individual cod of type s and age a in year y

$R_{y,s,a,p}$ is calculated using the formula

$$R_{y,s,a,p} = \frac{e^{0.13T_y} W_{y,s,a}^{0.26} S_{y,s,a,p} \ln 2}{\alpha_p (1.78 S_{y,s,a})^{0.52}}$$ (2)

where

T_y: Temperature (°C) at Eggum (68°22' N 13°38' E) at 100 m depth, in the end of March in year y.

$W_{y,s,a}$: Mean weight (kg) of cod age a of type s at 1 April in year y. The weights at 1 April were calculated assuming a linear growth throughout the year, i.e. a given cohort has the same weight growth increment in all quarters in a given year.

α_p: Prey-specific digestion (half-life) constant (in hours). The following prey groups were used in the calculations: Herring (*Clupea harengus*), Norway pout (*Trisopterus esmarkii*), other fish and invertebrates. In a few instances, poor cod (*Trisopterus minutus*) were found in the stomachs, and these were grouped together with Norway pout. The digestion rate for Norway pout and for other fish was assumed to be the same as for cod, while the digestion rate for invertebrates was assumed to be the same as for amphipods and krill. Values: Herring 88, Cod 84, Krill & amphipods 41.

$S_{y,s,a,p}$: Average stomach content (g) of prey p for cod age a and type s in year y

$S_{y,s,a}$: Average total stomach content (g) for cod age a and type s in year y

For NCC, age groups 4-8+ (age 8 and older) were used, while for NEAC, age groups 5-9+ (age 9 and older) were used. Fish younger than the minimum age (4 or 5 respectively) were included together with the fish in lowest age group.

The weight of each prey species and size group was adjusted by distributing the unidentified component of the diet proportionally among the various identified components, taking into account the level of identification. In order to investigate how much of the natural mortality of herring was due to cod predation, we calculated the biomass output for herring

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through natural mortality (MOB) (called the 'M-output biomass' by Hamre and Tjelmeland (1982), using the same approach as in Bogstad et al. (2000). In general, the MOB is calculated using the catch equation, but with F and M interchanged, and the calculated number removed by M is multiplied by a relevant mean weight:

$$MOB_y = \sum_a W_{y,a} \bullet \frac{N_{y,a} M_{y,a} (1 - e^{-(F_{y,a} + M_{y,a})})}{F_{y,a} + M_{y,a}} \quad (3)$$

where

MOB_y: M output biomass in year y

$N_{y,a}$: Number of fish of age a in the beginning of year y

$F_{y,a}$: Fishing mortality of age a fish in year y

$M_{y,a}$: Natural mortality of age a fish in year y

$W_{y,a}$: Mean weight of age a fish during year y

These data are taken from the latest assessment of Norwegian spring-spawning herring (ICES, 2006b). The mean weight $W_{y,a}$ is calculated as the average of the stock weights of this cohort at the beginning of years y and y+1, $w_{a,y}$ and $w_{y+1,a+1}$.

The herring found in the cod spawning area are almost exclusively age 3 and older , and those age groups 3-16+ were used in the calculations of MOB:

$$MOB_y = \sum_{a=3}^{15} \frac{(w_{y,a} + w_{y+1,a+1})}{2} \bullet \frac{N_{y,a} M_{y,a} (1 - e^{-(F_{y,a} + M_{y,a})})}{F_{y,a} + M_{y,a}} + \frac{w_{y,16} N_{y,16} M_{y,16} (1 - e^{-(F_{y,16} + M_{y,16})})}{F_{y,16} + M_{y,16}}$$

$$(4)$$

For age 3 and older herring, M is set to 0.15 for all ages and years.

Table and Figure text

Table 1. Sampling dates of stomachs, number of stations by gear and number of stomachs from spawning cod according to sex and cod type sampled on the Lofoten cruise 1996-1999 and 2001-2006.

Table 2. The number of stomachs sampled from large (> 50cm) North East Arctic cod on the winter survey in February and summer survey in August/September.

Table 3. Test statistics on the proportion of empty stomachs, Total Fullness Index (TFI) and Partial Fullness Index (PFI) for herring. Proc Mixed in SAS was used, with the station included as a random factor to account for dependencies within stations.

Table 4. Test statistics on the proportion of empty stomachs and Total Fullness Index (TFI), against season and year. Proc Mixed in SAS was used, with the station included as a random factor to account for dependencies within stations.

Table 5. Prey consumption by mature NEAC during the spawning period (1000 tonnes).

Table 6. Prey consumption by mature NCC during the spawning period (1000 tonnes).

Table 7. Herring M-output biomass (MOB) and cod consumption of herring (1000 tonnes).

Figure 1. Surveyed area for spawning cod, off the coast of the Lofoten peninsula (hatched area). The centers of mass of herring occurring in stomachs of cod by year is presented.

Figure 2. Number of cod in each 1 cm length group (points, with moving averages as lines) of spawning Norwegian Coastal Cod (NCC) and Northeast Arctic Cod (NEAC) males and females with stomach samples in Lofoten survey 1996-1999 and 2001-2006.

Figure 3. Observed values of proportion empty stomachs by sex, year and cod type.

Figure 4. Observed values of Total Fullness Index (TFI) by sex, year and cod type.

Figure 5. Diet composition (weight of prey, all stomachs combined) of spawning cod in Lofoten March-April 1996-1999 and 2001-2006. Upper panel: Norwegian Coastal cod, Lower panel: Northeast Arctic cod.

Figure 6. Partial Fullness Index (PFI) herring and unclassified fish by year

Figure 7. Length distribution of herring in cod stomachs (1 cm length intervals)

Figure 8. Estimates of proportion of empty stomachs with standard error bars in winter survey (Northeast Arctic (NEA) cod >50 cm February in Barents Sea), Spawning survey (spawning NEA cod in March-April in Lofoten area), and summer survey (NEA cod >50 cm in Svalbard area and Barents Sea in August –September).

Figure 9. Estimates of TFI with standard error bars in winter survey (Northeast Arctic (NEA) cod >50 cm in February in Barents Sea), spawning survey (spawning NEA cod in March-

April in Lofoten area), and summer survey (NEA cod >50 cm in Svalbard area and Barents

Sea in August –September).